

Communication in bottlenose dolphins: 50 years of signature whistle research

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Abstract Bottlenose dolphins (*Tursiops truncatus*) produce individually distinctive signature whistles that broadcast the identity of the caller. Unlike voice cues that affect all calls of an animal, signature whistles are distinct whistle types carrying identity information in their frequency modulation pattern. Signature whistle development is influenced by vocal production learning. Animals use a whistle from their environment as a model, but modify it, and thus invent a novel signal. Dolphins also copy signature whistles of others, effectively addressing the whistle owner. This copying occurs at low rates and the resulting copies are recognizable as such by parameter variations in the copy. Captive dolphins can learn to associate novel whistles with objects and use these whistles to report on the presence or absence of the object. If applied to signature whistles, this ability would make the signature whistle a rare example of a learned referential signal in animals. Here, we review the history of signature whistle research, covering definitions, acoustic features, information content, contextual use, developmental aspects, and species comparisons with mammals and birds. We show how these signals stand out amongst recognition calls in animals and how they contribute to our understanding of complexity in animal communication.

Keywords *Tursiops truncatus* · Animal communication · Individual recognition · Playback · Vocal learning

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Introduction

Although it has been known for a long time that dolphins are vocal animals, systematic study of their acoustic signals did not begin until the first captive bottlenose dolphins (*Tursiops truncatus*) became available for study in the United States. After initial descriptive reports (McBride and Hebb 1948), efforts concentrated on deciphering the meaning of single utterances, under the assumption that each whistle had a specific meaning, similar to words in a human language. These efforts led to a cataloguing of dolphin whistles (Dreher and Evans 1964) and some claims about linguistic capacities (Dreher 1961), but playbacks of whistles to dolphins only provided equivocal data on the possible meaning of signals (Dreher 1966; Caldwell and Caldwell 1977). In the early 1960's Melba and David Caldwell studied the vocalizations of bottlenose and common dolphins (*Delphinus delphis*) from a more traditional, biological perspective. They recorded recently captured animals and found that each individual had its own distinctive whistle type (Fig. 1) that it used in almost all contexts that they studied (Caldwell and Caldwell 1965, 1968). The Caldwells called these whistles “signature whistles” and hypothesized that they were used by conspecifics to identify the vocalizer (Caldwell and Caldwell 1968).

Subsequent studies have added to the initial results of the Caldwells, showing that dolphins use signature whistles primarily when separated from their conspecifics, and that in most animals, the signature whistle accounts for more than 90 % of all whistles emitted when the animal is in isolation (Caldwell et al. 1990; Janik and Slater 1998; Sayigh et al. 2007). This pattern has been reported for over 300 individual dolphins by a variety of researchers (reviewed in Sayigh et al. 2007). For freely ranging dolphins, 38–70 % of all whistles produced are signature whistles (Buckstaff 2004; Cook et al. 2004; Watwood et al.

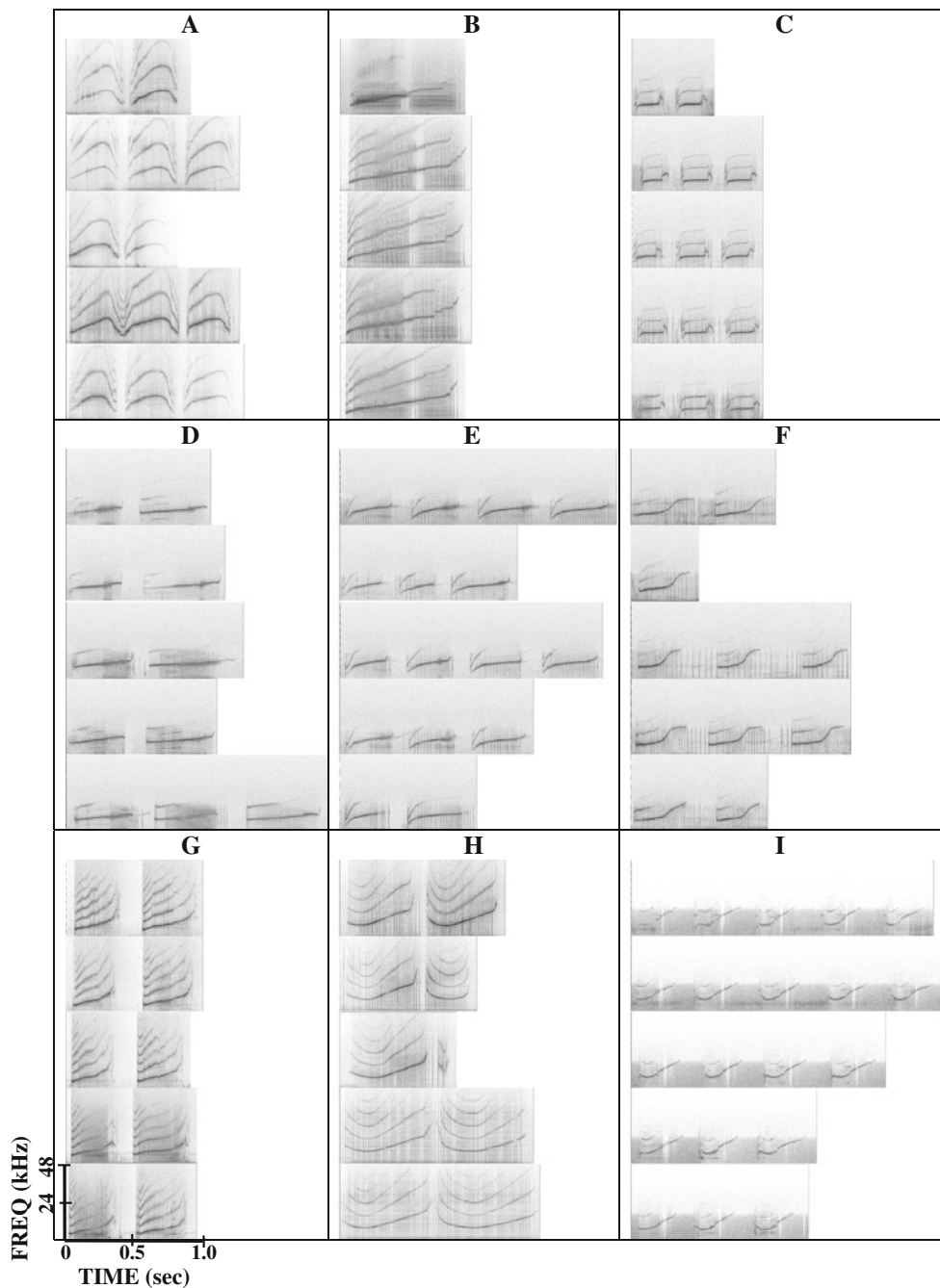


Fig. 1 Spectrograms of five whistles (numbers 1, 5, 10, 15, and 20 of 20 randomly selected whistles) from each of 20 randomly selected dolphins from the Sarasota Bay population. Frequency (up to 48 kHz) is on the *Y* axis and time (s) is on the *X* axis; identical time scaling

2005). Once developed during the first year of life, signature whistles usually remain remarkably stable throughout an animal's lifetime (Sayigh et al. 1990).

Studies on cognition discovered remarkable abilities in bottlenose dolphins, including the ability to copy novel sounds and use them to refer to objects (Richards et al. 1984), and the ability to understand the syntactic rules of an artificial signaling system based on the acoustic and

was used across the entire data set (reprinted from Sayigh et al. 2007 with permission from Elsevier). Each letter (A–T) indicates a box containing whistles from the same individual dolphin, with A being the first animal and T the 20th animal in our sample

hand signals (Herman et al. 1984). Furthermore, dolphins were found to copy signature whistles of conspecifics, potentially for the purpose of addressing them (Tyack 1986; Janik and Slater 1998). Copying is the reproduction of a received signal that the caller did not have in its repertoire before the copying event. We use the term “copying” here for every incident in which an animal is producing the signature whistle of another, even though

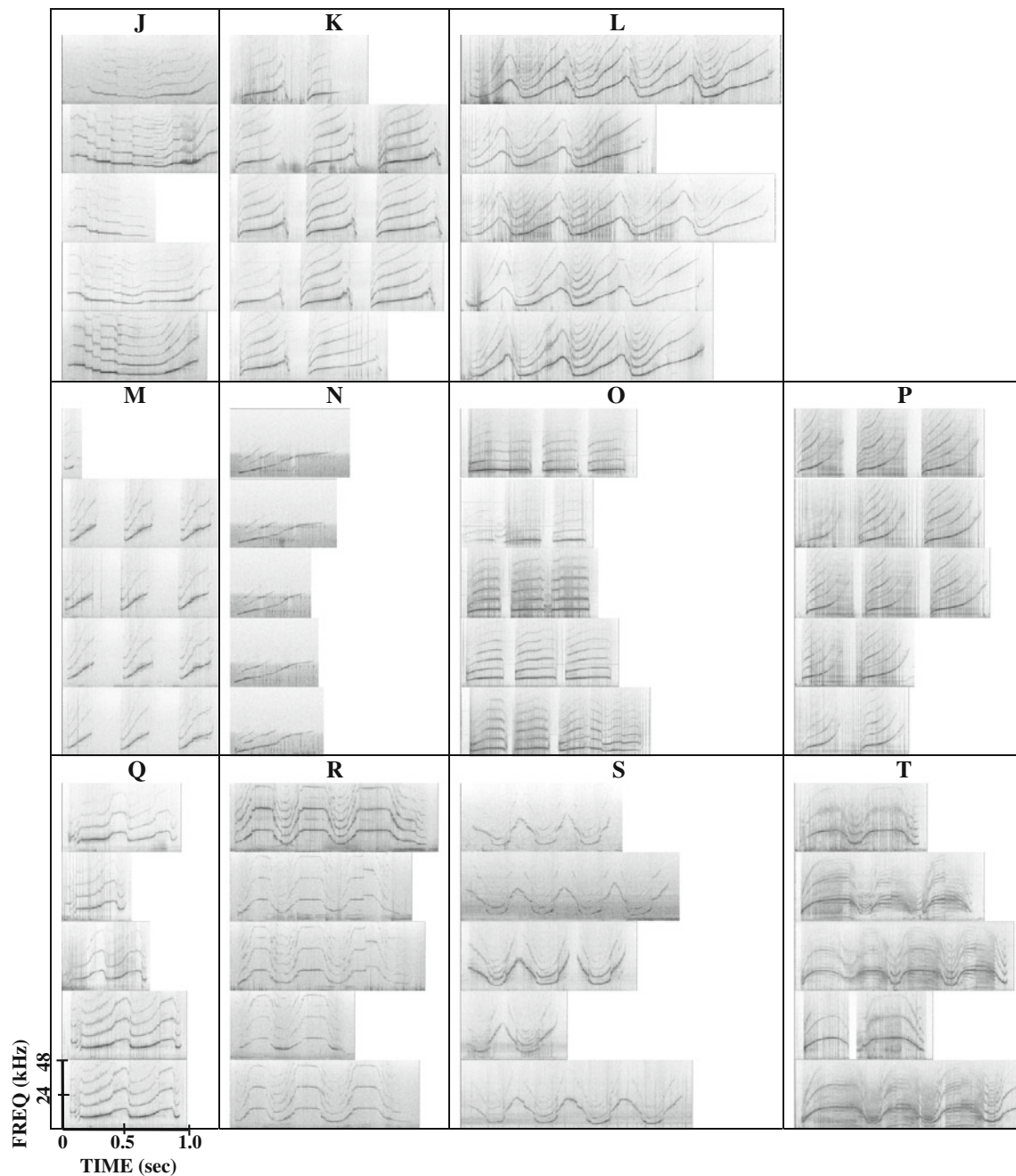


Fig. 1 continued

after the first production of a copy one could argue that this whistle is now part of the copier's repertoire. The terms "reference" or "referring to" indicate that a signal represents a specific object or entity. This requires that a mental representation or concept of the object is linked to the representation of the signal in the producer's and receiver's minds. This follows the ideas on meaning and reference presented by Hurford (2007) for animals.

Although delphinid communication is complex, with animals using large repertoires of whistles, clicks and pulsed sounds that are influenced by vocal learning (Janik 2009), the

signature whistle provided an accessible avenue to understand the communication of this cognitively advanced mammal. The relative stability and dominance of signature whistles in a dolphin's repertoire have enabled researchers to probe more deeply into the cognitive mechanisms involved in dolphin communication. In this review, we will present and evaluate our current knowledge on signature whistles and compare dolphin communication with that of other animals. This comparative approach will shed light on how similar cognitive and communicative abilities can evolve in taxa as diverse as dolphins, primates, parrots and song birds.

What are signature whistles?

Signature whistles have been defined both conceptually and operationally. The conceptual definition proposed by Caldwell et al. (1990) describes a signature whistle as the dominant whistle emitted by captive dolphins, which is individually distinctive and stereotyped in certain acoustic features. They hypothesized that the distinctive attributes of signature whistles function to broadcast the identity of the whistler (Caldwell et al. 1990). We propose a refined definition of a signature whistle as a learned, individually distinctive whistle type in a dolphin's repertoire that broadcasts the identity of the whistle owner. There are two important aspects of this definition that differ from that of the Caldwells. First, we incorporate the fact that signature whistles are developed via vocal production learning, wherein signal structure is modified as a result of experience with those of other individuals (Janik and Slater 1997). Vocal production learning does not require that a whistle type be copied from another animal (although this may occur), but only that the whistle development be influenced by auditory experience. Secondly, our definition refers to whistle types, which include all whistles of a particular frequency modulation pattern or contour. Thus, whistles of the same modulation pattern or contour belong to the same whistle type. In a vocal learner, the same whistle type can be produced by more than one individual, even though there may be inter-individual variation in parameters other than the frequency modulation pattern. One possible cause of such variation between callers could be voice cues, which arise from individual differences in the morphology of the vocal apparatus.

Operational definitions are useful when trying to identify signature whistles. A widely used method to find the signature whistle of an individual is to identify its most commonly produced whistle type in isolation. In fact, the contexts in which the Caldwells identified signature whistles were almost all isolation contexts (Caldwell et al. 1990). Another operational definition has been introduced recently, using the fact that signature whistles are usually produced in bouts (Janik et al. 2013). A bout analysis showed that if 75 % or more of whistles belonging to the same whistle type occurred within 1–10 s of another whistle of the same type, this whistle type was a signature whistle (Janik et al. 2013). The study compared signature whistles identified by isolating individuals to those from the same animals when they were swimming in groups. The cutoff of 75 % allowed a positive identification of 50 % of the emitted signature whistle types in the sample with no false-positive identifications.

Although signature whistles are often produced in bouts of several with an inter-whistle interval of 1–10 s, there appear to be no other consistent differences between

signature whistles and other whistle types, which are usually called non-signature or variant whistles. Although signature whistles are a dominant feature of dolphin communication, many non-signature whistles are produced as well, of which little is known about their possible functions. Signature whistles range from 1 to 30 kHz (Sayigh and Janik 2010) and have an overall duration of 0.1–4 s (Buckstaff 2004). The variability in specific parameters such as start frequency or bandwidth is similar to that found in non-signature whistles (Janik et al. 1994). Some signature whistles consist of repetitive elements called loops, which are usually separated by short gaps of up to 250 ms (Esch et al. 2009b). Some of these multi-looped whistles have distinctive introductory and/or terminal loops, so that one signature whistle can consist of two or more different short modulation patterns that almost always occur together as one unit. The much shorter interval between loops than between whistles makes a multi-looped structure easy to recognize in repetitive sequences.

Is it difficult to recognize signature whistles?

If bottlenose dolphins are isolated from their group, signature whistles usually account for between 80 and 100 % of all whistles. This has been confirmed by many studies with captive animals, where dolphins were separated by gates or removed from the water for veterinary examination, or with free-ranging animals that were temporarily captured (Caldwell and Caldwell 1965; Burdin et al. 1975; Caldwell et al. 1990; Sayigh et al. 1990, 1995, 2007; Janik et al. 1994; Janik and Slater 1998; Watwood et al. 2004; Esch et al. 2009b). Signature whistles also show great inter-individual variation and much smaller intra-individual variation (Janik et al. 1994), making their spectrograms easy to classify by eye (Fig. 1). Owing to this relatively obvious pattern, human observers have often been used to classify signature whistles. In blind classification studies, humans reliably group together whistles produced by the same individual even if they have no knowledge of who produced the whistles (Janik 1999; Sayigh et al. 2007). This is convincing confirmation that classification of whistles by human observers is a valid method to use. Similar to studies in bird song, this has become the standard over the years. Computer methods can also be used to classify whistles correctly (e.g. Deecke and Janik 2006). However, due to the fact that the exact whistle parameters show some variation and that bottlenose dolphins occasionally stretch or compress the overall modulation pattern of signature whistles in time, these methods need to be fairly sophisticated. McCowan and Reiss (1995a) used a computerized classification method that ignored differences in duration of whistles when classifying them. Later

studies showed that this method does not accurately classify signature whistles (Janik 1999; Sayigh et al. 2007). In addition to the problems with whistle classification in the McCowan and Reiss (1995a) study, there were also problems with the methods that they used to attribute whistles to individual vocalizers. By focusing on whistles associated with the release of bubble streams from an animal's blowhole, they concluded that there were no signature whistles in their samples. However, Fripp (2005) showed that bubble streams are primarily seen when animals produce so-called “upsweep” whistles, so that using bubble streams for identifying whistles leads to a biased sample. In addition, McCowan and Reiss (1995a) studied animals swimming together in the same pool, a context in which animals acclimatized to captivity often do not produce signature whistles (Janik and Slater 1998). Thus, the McCowan and Reiss (1995a) study could not have found signature whistles even if the animals had produced them. Unfortunately, the problems with these methods make it difficult to interpret the results of studies in which they were used (e.g. McCowan and Reiss 1995a, 1995b).

In a later study, McCowan and Reiss (2001) questioned the existence of signature whistles again, claiming that they had now replicated the contexts of previous signature whistle studies, namely the isolation context. However, one of the contexts in their study was called “isolation in the same pool” which contradicts the claim that the animals were isolated. It was unclear how much of their data came from this context. McCowan and Reiss (2001) also did not provide data on how long animals were put into the contexts that they labeled as isolation. Janik and Slater (1998) pointed out that bottlenose dolphins accustomed to captivity often need to be isolated for long periods of time before they produce signature whistles. Interestingly, the one animal that McCowan and Reiss (2001) did take out of the pool seemed to produce signature whistles as predicted by previous studies. A re-analysis of signature whistle data from capture sessions of wild animals in reply to the McCowan and Reiss (2001) paper (Sayigh et al. 2007) reconfirmed the existence of signature whistles, a fact later also acknowledged by McCowan and Reiss (Marino et al. 2007). Thus, these studies emphasize that while signature whistles are easy to recognize, the correct methods need to be used for their identification.

How do signature whistles develop?

Signature whistles emerge early in life, with most calves showing a crystallized signature within the first 3 months of life (Caldwell and Caldwell 1979). Studies on vocal learning in whistles (e.g. Richards et al. 1984) are suggestive that whistle development is influenced by experience. Cross-fostering or isolation experiments with

dolphins are rarely possible due to their highly social life styles and such experiments are likely to disrupt development on many levels making the interpretation of results difficult. However, two anecdotal reports describe how the signature whistles of two dolphin calves resembled those of pool members that were not their mothers. In one case, a stranded calf changed its signature to resemble that of its foster mother (Tyack and Sayigh 1997), and in another a calf copied the whistle of a Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) with which it was housed (Caldwell and Caldwell 1979). Miksis et al. (2002) found that bottlenose dolphins born in captivity tend to have less modulation in their signature whistles than do wild dolphins, and they hypothesized that this is due to the frequent use of unmodulated whistles as a bridge signal during training of animals in captivity. If the animals used signals in their environment as models for the development of their signature whistles, the bridge would be an obvious model. The best evidence for the influence of learning on signature whistles comes from observational work. In the Sarasota, Florida, USA, dolphin population, the majority of bottlenose dolphin calves develop signature whistles that are not similar to those of their mothers, but among those that do show such similarities, more are males than females (Sayigh et al. 1995) and such a differential pattern between the sexes and the general lack of similarity in whistles between mothers and offspring suggest a decreased genetic influence on whistle development. Additional work with the Sarasota dolphin population suggests that signature whistles are modeled after whistles of conspecifics and then modified to produce a novel and unique signature (Fripp et al. 2005). In their study, Fripp et al. (2005) compared signature whistle structure of five calves to those of their associates, and found that in four cases, the calves' signature whistles were unlike those of their mothers, and most closely resembled those of relatively rare associates of the mother. The fifth calf developed a relatively simple “upsweep” type whistle that was highly similar to that of its mother as well to those of two rare associates. To show that these were not accidental resemblances, Fripp et al. (2005) also compared the calves' whistles to those of another population and found that calves were significantly more likely to develop whistles similar to those of animals in the Sarasota population.

Once a signature whistle has crystallized, very few factors can change its overall modulation pattern. Female signature whistles remain stable for decades (Sayigh et al. 1990, 2007) and so far there is no reported evidence for a change. In males, signature whistles can change to resemble the whistle of an alliance partner. Alliances are relatively stable social units in which two or more males cooperate when competing with other males (Connor et al. 2001). In such cases, each individual still retains

individually specific aspects of the signature whistle modulation pattern, but whistles of males belonging to the same alliance become more alike (Smolker and Pepper 1999; Watwood et al. 2004).

What information is encoded in signature whistles?

The original hypothesis that signature whistles are used for individual recognition has been upheld by both experimental and observational work. Signature whistles are usually only produced when animals are out of visual contact (Janik and Slater 1998), which suggests such a function. However, the main evidence for individual recognition comes from playback studies. Bottlenose dolphins turned more towards a speaker playing signature whistles of a close relative than to whistles of a familiar associate (Sayigh et al. 1999). Janik et al. (2006) found the same pattern in playbacks of synthetic whistles that lacked potential voice cues, but preserved the modulation pattern of the signature whistle, thus demonstrating that identity information is encoded in the modulation pattern (Janik et al. 2006). This is remarkable given that each animal develops its own, novel modulation pattern through vocal learning after hearing the whistles of others. Janik et al. (2006) could not find any evidence for kin specific modulation patterns, even though some calves have signature whistles that are very similar to those of their mothers (Sayigh et al. 1995). However, even in those cases, the signature of the mother and the calf are not the same. Therefore, it appears that the signature whistle is truly an arbitrary signal that is introduced into the dolphin communication system, through vocal learning, by its owner.

Although identity is the most obvious information encoded in signature whistles, with large inter-individual differences in modulation patterns, other information is also encoded. Subtle parameter variations that preserve the overall modulation pattern, but change, for example, the start frequency or bandwidth of the whistle, encode motivational information (Janik et al. 1994). Furthermore, whistle rate gives information on stress levels in bottlenose dolphins, with rates being higher when water levels are lowered in a pool or animals are temporarily captured (Caldwell et al. 1990; Esch et al. 2009a). Signature whistle rates in freely ranging animals are low, with means of 0.06–0.4 whistle per min and long periods of silence (Buckstaff 2004; Watwood et al. 2005; Esch et al. 2009a), while means of 10.9 (King et al. 2013) to 14.3 whistles per min (Esch et al. 2009a) have been found during capture-release projects. Other contexts in which signature whistle rates increase is when animals meet at sea (mean $\pm$ SD: 4.6 ± 1.5 whistles/min) (Quick and Janik 2012) and shortly before a boat passes close by a group

(mean = 1.4 whistles/min) (Buckstaff 2004). High whistling rates have also been observed during reunions of mothers and calves (Smolker et al. 1993). The overall mean whistle rates per individual (signature and non-signature whistles) of free swimming animals range from 1 whistle/min when travelling to 9.8 whistles/min when engaged in non-polarised movement as found during socializing (Quick and Janik 2008).

Do dolphins copy signature whistles of others?

Bottlenose dolphins are remarkably skilled at vocal copying (Richards et al. 1984). It is therefore not surprising that they are capable of copying signature whistles of others. This was first discovered in two captive animals that appeared to have two shared, stereotyped whistles (Tyack 1986). Because each of these whistles was primarily produced by one of the dolphins, Tyack interpreted his findings as evidence for signature whistle mimicry, in which one animal tried to address the other by copying its signature whistle. Tyack was unable to record the animals in isolation, but attached a tag to each of them with LED's that lit up when the sound exceeded a certain level. This allowed the identification of the calling animal. A later study after one of the animals had died confirmed that the remaining animal produced only one of the whistles in the absence of its tank-mate (Tyack 1991), confirming Tyack's earlier interpretation. Subsequently, whistle copying has been found in other captive and wild bottlenose dolphins (Sayigh et al. 1990; Tyack and Sayigh 1997; Janik and Slater 1998; Janik 2000; King et al. 2013). In captive animals, whistle copying generally occurs at very low rates of 0.007–0.04 copies/min/individual (Janik and Slater 1998; King et al. 2013). During capture-release events, wild animals produced copies at a rate of 0.18 /min/individual (King et al. 2013). However, this was the rate for capture-release events during which at least one occurrence of copying was recorded; an overall rate would be lower. The exception to these low rates is Tyack's (1986) study, where copying reached up to 0.3 copies/min (Tyack 1986). The actual rate was likely higher, since Tyack could only identify the caller for 57 % of all whistles. A possible explanation for this high rate may be the tag used to identify callers. The animals may have tried to manipulate each other's vocal output after seeing the light come on, which could have influenced their copying rates.

The fact that dolphins can copy signature whistles raises the question of how a whistle can indicate the identity of an individual, when it is also produced by others. Copies should make the signal less specific to an individual and therefore cause confusion. However, copying is rare and

copies are usually recognizable as copies. Individuals change specific parameters in the copied call, so that it stands out as a copy (Tyack 1991; King et al. 2013). Thus, copying does not destabilize the recognition function of the call.

How are signature whistles and their copies used?

Although signature whistles account for almost 100 % of all whistles when bottlenose dolphins are isolated from group members (Caldwell et al. 1990), they make up only around 38–70 % when animals are swimming freely in the wild (Buckstaff 2004; Cook et al. 2004; Watwood et al. 2005). In close proximity, as can be the case in captivity, they are often not used at all (Janik and Slater 1998). Free-swimming males produce more signature whistles when alone compared to when they are with their alliance partner (Watwood et al. 2005). These usage patterns support the idea that signature whistles are used for recognition and group cohesion (Janik and Slater 1998). Dolphins also engage in vocal exchanges using signature whistles (Sayigh et al. 1990; Janik and Slater 1998; Nakahara and Miyazaki 2011). In the wild, such exchanges occur when groups meet at sea before joining each other (Quick and Janik 2012).

In playback experiments, bottlenose dolphins tend to respond to signature whistles of group members with their own signature whistle (Nakahara and Miyazaki 2011). However, occasionally they will copy the whistle that they just heard (Nakahara and Miyazaki 2011). Whistle copying between dolphins has primarily been documented in such vocal matching interactions, in which one animal copies a signature whistle shortly after it has been produced by the signature whistle owner (Janik and Slater 1998; King et al. 2013). Copying tends to occur between mothers and their dependent offspring and between members of male alliances (King et al. 2013). This pattern suggests that it is primarily an affiliative signal. However, a study on whistle matching in the wild found patterns of copying in which animals frequently overlapped one another's whistles, and up to three individuals matched one another (Janik 2000). These patterns suggest other contexts of matching. Some of these interactions could have involved non-signature whistles, but the use of non-signatures in matching appears to be rare (King et al. 2013). In most cases of copying, the match appears to be a reply to the animal calling its signature whistle as if to confirm that it has been received. However, Watwood et al. (2005) found that whistles produced by wild bottlenose dolphins regularly resemble the signature whistles of animals not in their group. This hints at whistle copying as a means to locate specific individuals.

Do all dolphins have signature whistles?

Signature whistles seem to be particularly prominent in common bottlenose dolphins, but evidence exists for other species too. There is evidence for signature whistles in Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) (Gridley et al. 2013), common dolphins (Caldwell and Caldwell 1968), Atlantic spotted dolphins (*Stenella plagiodon*) (Caldwell et al. 1973), Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) (Caldwell and Caldwell 1971), Pacific humpback dolphins (*Sousa chinensis*) (van Parijs and Corkeron 2001), Guiana dolphins (*Sotalia guianensis*) (de Figueiredo and Simão 2009), and one non-delphinid, the narwhal (*Monodon monoceros*) (Shapiro 2006). Pilot whales (*Globicephala macrorhynchus*) have very complex vocal repertoires, but evidence is suggestive of signature whistles (Sayigh et al. 2013). However, not all delphinids have signature whistles. Killer whales (*Orcinus orca*) are perhaps the best known example of a species that does not produce signature whistles. While they produce whistles, they seem to primarily use burst-pulsed sounds in social interactions (Ford 1989). These call types are shared within pods rather than being specific to individuals (Miller and Bain 2000), even though they have individually distinctive features that are akin to the voice cues found in other mammals (Nousek et al. 2006).

How and why are signature whistles different from recognition calls in other animals?

Recognition calls are important for many animals, including a variety of isolation or contact calls described in the literature. Many recognition calls use by-product distinction that is caused by individual differences in the morphological tract or exact generation pattern that animals use for their calls (Boughman and Moss 2003). Such by-product distinctiveness affects all calls that an animal produces. The fact that a specific isolation call is used indicates the context of the caller but is not necessary for encoding the identity information.

One of the most impressive recognition systems can be found in the display calls of penguins. Penguins that do not build nests and have mobile chicks use frequency and temporal parameters for vocal recognition, especially relying on a two-voice system that creates individually distinctive beat patterns (Aubin et al. 2000). These distinct features in penguin calls are also often called signatures, but it is unclear how they develop. The need for individual recognition likely drove the evolution of phenotypic variability (Tibbetts and Dale 2007). Such variability can be achieved through increasing inter-individual variation in the morphology of the vocal apparatus, or alternatively

through the evolution of vocal learning (Janik and Slater 1997). In the development of signature whistles in dolphins, learning is an important contributing factor; in penguins the mechanism is less clear.

However, learned recognition calls are known to occur in several bird species. Zebra finches (*Taeniopygia guttata*) (Zann 1990) and green-rumped parrotlets (*Forpus passerinus*) (Berg et al. 2011a), for example, learn the structure of their contact signals from their fathers or parents and as a result sound like them. These calls are later used for individual mate recognition (Vignal et al. 2004; Berg et al. 2011b). Bottlenose dolphins stand out from these examples in that their calls are more individually specific than those of birds, since they do not usually show the same level of similarity with a tutor. Vocal learning is used differently here, since dolphins usually significantly modify whistles that serve as models in signature whistle development or at times appear to invent a novel whistle rather than to copy one in its environment. Dolphins appear to use experience to avoid closely matching a model while birds tend to copy the model. This raises the question of how individual recognition with bird contact calls is possible if siblings sound alike. Some birds achieve this by varying the composition of their song repertoires (Beecher et al. 1994), a method rather different from using individually specific signals for recognition. It is possible that the parameters that maintain individual recognition in bird contact calls are in fact not influenced by learning but are due to by-product distinctiveness, while the learned parts of bird contact calls may allow for kin recognition. Alternatively, birds may use a similar mechanism as dolphins to introduce parameter variations that are different from the ones they hear from conspecifics. This could involve inventing novel calls or learning to copy a signal, but then introducing individually distinctive variation. Evidence for the former mechanism is available for grey catbirds (*Dumetella carolinensis*) (Kroodsmma et al. 1997) and for the latter for song sparrows (*Melospiza melodia*) (Nordby et al. 2007). Not surprisingly, grey catbird repertoires show inter-individual differences that are comparable to those found in bottlenose dolphin signature whistles. Orange-fronted conures (*Aratinga canicularis*) may also use learning in the same way as dolphins since individuals tend to have several individually distinctive signature calls that differ in their frequency modulation patterns (Cortopassi and Bradbury 2006). However, generally the inter-individual differences in contact calls of birds are considerably smaller than those found in bottlenose dolphin signature whistles.

Group recognition calls of birds, however, can show large differences (Mundinger 1970; Mammen and Nowicki 1981; Brown and Farabaugh 1997), the group-specific contact calls of budgerigars (*Melopsittacus undulatus*) are perhaps the best example here. To arrive at these, group

members modify the frequency modulation pattern of their contact call (Hile et al. 2000). A similar case in mammals can be found in group-specific calls of greater spear-nosed bats (*Phyllostomus hastatus*) (Boughman 1998). Clearly, copying others is a large factor here and choosing a similar model is what leads to group-specific calls. In that sense, this kind of convergence is not similar to what is found in signature whistle development in dolphins. However, the vocal convergence found in adult dolphin alliance members (Smolker and Pepper 1999; Watwood et al. 2004) is perhaps a parallel. It is an open question whether birds or bats ever address another group by copying their call as dolphins do when copying signature whistles of individuals.

The closest parallel to signature whistle copying in dolphins can be found amongst parrots. Orange-fronted conures copy the individually distinctive calls of conspecifics, and animals that are addressed in this way tend to reply more quickly and with higher call rates than they do to calls that do not resemble their own (Balsby and Bradbury 2009; Balsby et al. 2012). Spectacled parrotlets (*Forpus conspicillatus*) also produce copies of calls of conspecifics when they see them (Wanker et al. 2005). More anecdotal evidence for this has been reported for bou-bou shrikes (*Laniarius aethiopicusmajor*) (Thorpe and North 1966) and for ravens (*Corvus corax*) and white-rumped shamas (*Copsychus malabaricus*) (Gwinner and Kneutgen 1962). Vocal addressing of conspecifics is also common in songbirds through vocal matching, where one male repeats the song of another shortly after it was given (Catchpole and Slater 2008). This is a very effective way of addressing and leads to a clear reaction in the matched individual. However, song types are shared by many individuals and the same song types can be used to address different individuals when matching them. The addressing in matching occurs because of the close temporal proximity between the call and the match and not because song types indicate caller identity. Furthermore, in song birds, song matching is an aggressive signal and represents a step in the escalation of interactions (Searcy and Beecher 2009). Although dolphins do not produce song, whistle copying in dolphins can also occur in matching interactions, usually as a brief reply after a whistle owner has produced its signature whistle. However, in dolphins, copying is primarily an affiliative signal between close associates (King et al. 2013).

Because dolphin signature whistles are so individually distinctive, it is possible to ask when animals use them outside of direct interactions with the call owner. In a wild population, dolphins were found to sometimes produce whistles resembling the signature whistles of absent individuals (Watwood et al. 2005). This is an interesting observation, but we do not know the function of this use of signature whistle copies. The most likely reason for it is that dolphins use copies of signature whistles when they

are searching for a specific individual. Such a use of labels in the absence of the whistle owner raises the question of how signature whistles are connected to a mental representation of a conspecific.

Extensive research into cognitive abilities of bottlenose dolphins allows us to consider what cognitive mechanisms might be involved in the production of signature whistles and their copies. The most relevant work here includes experiments in which novel sounds were paired with objects in captivity. Herman et al. (1984) trained a bottlenose dolphin to understand the association between novel sounds and objects and tested the animal's ability to understand syntactical information in organized sequences of these sounds. He used the same approach with another individual using gestural instead of acoustic signals. One of these animals was also capable of using acoustic signals to label objects (Richards et al. 1984) and to report whether the object that the sound represented was present or absent in the pool (Herman 2006). Harley (2008) showed that bottlenose dolphins can learn to associate signature whistles with whistle producers. She paired each of six paddles with a different signature whistle that was recorded in the wild, and trained a dolphin to approach the correct one when the corresponding signature whistle was played. Another study in captivity demonstrated that dolphins produce sounds that were paired with objects spontaneously when they manipulated them (Reiss and McCowan 1993). All of these findings taken together suggest that signature whistles refer to individuals in a dolphin's mind, opening up the possibility that signature whistle copies are referential labels for individuals.

Conclusions

The bottlenose dolphin signature whistle clearly is a specific adaptation to ensure individual recognition and social cohesion in a fission–fusion society, where individual rather than group recognition has the highest priority. It is likely that vocal learning evolved in this taxon due to the needs of maintaining and negotiating contact in a noisy environment where sound is the only viable communication channel (Janik and Slater 1997). It remains an unresolved question whether advanced cognition in dolphins evolved in the context of using sounds in a sophisticated way to explore and manipulate their biological and social environments or whether selective pressures for more general skills were responsible. Leaving this question aside, bottlenose dolphins are an interesting study species since they combine many cognitive abilities of the great apes with the communicative versatility that comes with vocal learning (Janik 2013). Further studies are needed to explore how these factors interact and how dolphin communication skills compare to those of the only primate

capable of vocal learning, ourselves. When the Caldwells started their signature whistle research 50 years ago, it may have seemed like a less complex signal than what was expected from dolphins at the time. As we have seen though, the signature whistle turned out to be a fascinating case in which each animal introduces a novel call into an existing communication system that is then copied by others to address the whistle owner. Further research is needed to assess how unique this pattern is amongst animals in general, and to investigate underlying cognitive mechanisms for this behavior.

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